Invasiveness of brook charr (*Salvelinus fontinalis*) in small boreal headwater streams

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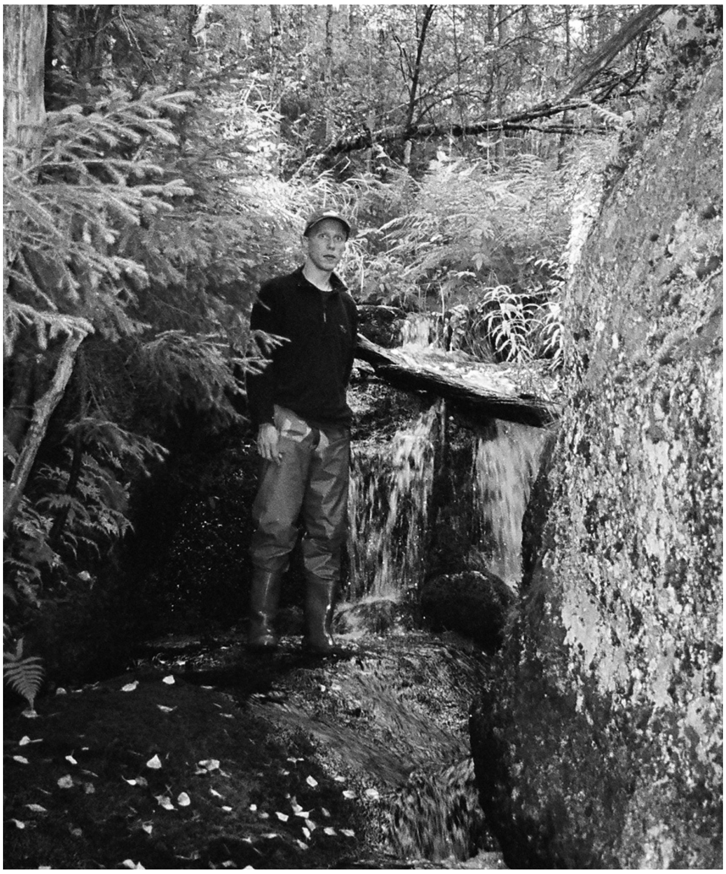

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Contents

Abstract
Invasion of the introduced North American species brook charr (*Salvelinus fontinalis*) is believed to threaten the native aquatic fauna in Swedish streams and lakes. Although introductions have been made since 1892 and the species is widely spread in the country, little is known about invasion dynamics and patterns. The ability of brook charr to disperse upstream through small boreal streams was investigated with electro-fishing. The study includes 18 headwater streams with documented time and place of stocking. Vertical water falls up to 1,3m and complex falls up to 1,15m had been ascended. Slopes with gradients up to 22%, measured with clinometer in the field and 31% measured in ArcGIS did not stop the upstream invasion. The obstacles that turned out to be barriers were: areas with subsurface stream flow through boulders (3,5-100m), a four-meter long plug of debris/sediment and a 65m long steep (22,6%) flat rock. Very small streams with mean annual discharge as low as 2,5*l*/s have been invaded. The invasion rate, in streams without barriers to invasion, ranged from 19,7 – 71,2 m/year, with a mean of 48 m/year. Increase in mean annual discharge (27-171*l*/s) and total stream gradient (0,56-4,30%) significantly increased the invasion rate. If charr had been introduced in a lake or a stream did not affect the invasion rate. Neither did the presence of brown trout in the streams or the number of repeated stockings.

Introduction
Introduction of non-native species is one of the most severe environmental threats on biological diversity today (Stachowicz et al. 2002). In freshwater ecosystems, interactions with non-native fish species are one of the leading causes of native species being wiped out or declined (Kruse et al. 2000). Sweden has reproducing populations of six different introduced fresh water fish species, five of which are salmonids (Swedish Environmental Protection Agency 2003, Swedish national board of fisheries 2003). Since non-native salmonids are biologically similar to native salmonids, there is a potentially big risk for niche overlap and interspecific interactions (Dunham et al 2003). Of the five introduced salmonid species, the brook charr (*Salvelinus fontinalis)*, a charr native to eastern North America, is the most successful (Swedish national board of fisheries 2003).

Brook charr (or brook trout) has been introduced by man to Swedish streams and lakes since 1892 (Filipsson 1994; Swedish national board of fisheries 2003) and is now widespread in the country. Stocking still occurs but not at the same extent as earlier. In 1995–2001, 35 to 50 stockings were made annually (Swedish national board of fisheries 2003) and since the 1930´s very few new fishes have been imported from North America (Aqualiens 2002). Brook charr have been found to prefer low-gradient, cold-water streams (Larscheid and Hubert 1992), but also appear to be well adapted to steep stair-stepped sections (Larson et al. 1995). Bozek and Hubert (1992) presented a model by which they were able to predict the presence of charr with 87% certainty, and classified charr as a high elevation, low gradient and narrow-stream species. A study with marked fish by Adams et al (2000) showed that charr could ascend steep channels with slopes of 13% that extended for more than 67m and 22% for 14,5m, they were also able ascended a 1,1m high vertical fall and a 1,5m high complex fall.

Brook charr invasion of streams and lakes, in the United States and Canada, has caused a decline of native salmonid species (Dunham et al 1999), reptiles (Matthews et al. 2002), amphibians (Knapp and Matthews 2000) and invertebrates (Carlisle and Hawkins 1998; Schindler et al. 2001) and also an increase in algae production (Schindler et al. 2001). This species is thought to have similar negative effects on the Swedish, native, brown trout (Swedish national board of fisheries 2003) and most likely on other organisms, especially in historically fishless habitats (Schindler et al. 2001). It is therefore important to get an understanding of what habitats charr are able to colonize. Even so, few studies on brook charr have been made in Sweden and little is known about its invasion patterns. Dunham et al. (2003) suggests that rates and patterns of invasion by brook charr likely depend on two factors: positive population

lation growth in source populations and the ability to disperse through hydrologic networks to locate and colonize new habitats.

The aim of this work was to identify the distribution front in 18 headwater streams in Västernorrland and to study the invasive ability of brook charr in these streams. I was also interested in the factors influencing the invasion rate and to define absolute obstacles to dispersal. The following predictions were made:

- Since it is commonly considered that brook charr densities decrease with increasing gradient (Chisholm and Hubert 1986; Fausch 1989; Larscheid and Hubert 1992), the invasion rate would decrease in the same way.
- Because charr appear to be limited by low stream flow and wetted width (Nelson et al. 1992), the invasion rate should increase with increasing discharge.
- The invasion rate should increase with the number of stockings.
- Brook charr would not be able to disperse through slopes steeper than 22% (20m long) or waterfalls higher than 2m (Rich et al. 2003).
- Since small, steep headwater stream segments often are the last refuges of native salmonid populations when confronted with introduced species (Fausch 1989; Larscheid and Hubert 1992; Adams 2000) it was expected to find refuges of native brown trout in some streams.

Material and methods

Study area

The study includes 18 small boreal streams (stream order 1-3), detected in post-stocking surveys prior to this (Spens *in prep*), in four different drainage areas that discharge into the Baltic Sea (Table 1). All streams are located in the northern parts of the county Västernorrland, central Sweden (fig 1). The studied reaches are located at elevations from 70 to 400 meters above sea level. Västernorrland is dominated by bedrock that is hard to decompose, which makes the area vulnerable to acidification (Söderberg and Norrgrann 2001). The county covers an area of 21 678 km^2 and is sparsely populated (11 persons/km^2) (County Administrative Board of Västernorrland 2003).

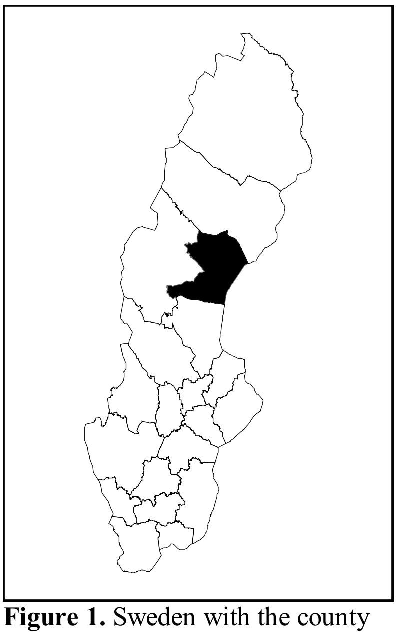

Figure 1. Sweden with the county Västernorrland in black.

Streams that met the following criteria were included: (a) populations of *Salvelinus fontinalis* was previously documented (Spens *in prep*), (b) small headwater streams, (c) documented year and place of introduction (Spens *in prep*), (d) the fish had been introduced either in the lower parts of the stream or in a downstream lake (Spens *in prep*) and (e) dispersal status in the upper parts of the stream were unknown.

Table 1. The four main drainage areas and the studied streams. The discharge is a mean based on the mean annual specific discharge into the Baltic Sea for the period 1931–2000 (SMHI).

Drainage area	1. Huså n	2. Gideälven	3. Moälven	4. Nätraån
Drainage area (km^2)	578	3442	2307	1024
Mean annual discharge (m^3/s)	6,2	35,0	24,0	11,3
Studied streams	1. Kallån 2. Halvförensbäcken 3. Långsmalbäckens tillopp 4. Hemsjöns tillopp	1. Uddersjölidbäcken 2. Maddmyrbäcken 3. Kroktjärnsbäcken 4. Rödtjärnsbäcken 5. Lammtjuvbäcken	1. Lövlidbäcken 2. Skavarsbäcken 3. Billabäcken 4. Järbäcken 5. Nipbäcken (east) 6. Nipbäcken (west) 7. Malmtjärnsbäcken	1. Sjunkmyrbäcken 2. Rössjöbäcken

Table 2. Stream and stocking data. Drainage area, mean annual discharge and stream order at the position of stocking.

Stream	**Drainage area (km^2)**	**Mean annual discharge (*l*/s)**	**Stream-order**	**Year of stocking**	**Number of stockings**	**Place of stocking**
Kallån	15,55	171	3	1958	1	stream
Halvförensbäcken	2,78	31	2	1964-76	4	lake
Långsmaltjärns tillopp	2,65	29	1	1957-66	4	lake
Hemsjöbäcken	0,76	8	1	1945-80	10	lake
Uddersjölidbäcken	1,62	18	2	1926-80	17	lake
Maddmyrbäcken	6,20	68	3	1926-80	17	lake
Kroktjärnsbäcken	2,01	22	2	<1968	No data	lake
Rödtjärnsbäcken	1,13	12	2	1926-51	5	lake
Lammtjuvbäcken	2,89	32	2	1950	1	stream
Lövlidbäcken	2,58	28	2	1950-57	2	lake
Skavarsbäcken	4,81	53	3	1950-57	2	lake
Billabäcken	1,60	18	2	1962-64	4	lake
Järbäcken	7,95	88	2	<1930	4	stream
Nipbäcken (east)	4,21	46	2	1949	1	lake
Nipbäcken (west)	4,21	46	2	1949	1	lake
Malmtjärnsbäcken	2,49	27	2	1949	1	lake
Sjunkmyrbäcken	5,96	66	3	1951-66	7	stream
Rössjöbäcken	21,75	239	3	1951-66	7	stream

Data collection

The electro-fishing was conducted from 2003-09-05 – 2003-10-16. Water temperatures varied from 12,4°C in the start and 3,4°C in the end of the study. The electro-fishing was performed using a Biowave II backpack electro-fisher, version: 2,05 providing a pulsed DC of 400 – 600V. Only one person performed the fishing in each stream to avoid errors. Fishing started at a co-ordinate that was known to be the most upstream observation of brook charr in each stream (Spens *in prep*). As no similar study has been done in these streams before, the co-ordinate can not be used as an indicator of the earlier dispersal front. Fishing continued until

(a) the stream was dry, (b) it ended in a headwater lake or a mire, or (c) no observation of brook charr in at least 120m of good fish habitats (suitable spawning areas and pools) was done. The fishing was quantitative and no densities were estimated. Individuals of all caught fish species were measured to the nearest 5mm. To identify absolute obstacles and get an understanding of how smaller obstacles affect the invasion rate, all obstacles were noted and measured. The height of waterfalls was measured from surface to surface with a folding rule. The height and the length of rocks and bolder areas with subsurface stream flow and other obstacles such as beaver dams were measured in the same way. A clinometer was used to measure the height and a measuring tape to measure the length of slopes. A gradient in percent was calculated as follows (Markusson et al. 1997):

$$\boxed{\frac{\text{Slope height (m)} * 100}{\text{Slope length (m)}}}$$

Area analyses in ArcGIS 8.1
The sizes of the drainage areas (km^2) from the place of stocking and from the co-ordinate of the last caught brook charr were measured with elevation grids. The mean annual discharge for each stream was then calculated by multiplying the drainage area with the mean annual discharge (11*l*/s) (SMHI 1990) for Västernorrland. By using ArcGIS, the length of the invaded reaches from the location of stocking were measured. The gradient of the invaded reaches was measured from the elevation grids. Measuring of gradient between 5-meter elevation iso-lines (contours) identified the highest ascended slope in each stream. The identification of obstacles is more accurate this way, than if a certain distance always is measured when calculating the gradient (Spens *in prep*).

Data analyses
Statistical analyses were made in Systat. Since the year and place of stocking was known, the invasion rates as meters/year could be calculated. In streams with consecutive stockings, the first year of stocking was used. The difference in invasion rate in streams with and without barriers was compared using a non-parametric Mann-Whiney U test. The observed variation in invasion rate between streams without barriers in front was tested using step-wise multiple linear regression analysis, with (a) mean annual discharge at the place of stocking, (b) mean annual discharge in the position of the last caught charr, (c) stream gradient, (d) the steepest ascended reach, measured in ArcGIS and (e) the number of stockings, as independent variables. The effect of presence of trout, detected during the electro-fishing, and the place of stocking (stream or lake) on invasion rate was tested using t-tests.

Results

Electro-fishing

Results from the electro-fishing are presented in table 3. Besides the number of caught fishes of each species, the number of observed fishes is shown. These are individuals that were identified as charr or trout but not caught. Only brown trout and brook charr are noted, since the number of individuals of other species was very small. Trout and charr were sympatric in five of the streams and charr were allopatric in 14 of the electro-fished distances.

Table 3. Results from the electro-fishing. Observed fishes are individuals that could be identified as charr or trout although they were not caught. The mean lengths are calculated from the caught fishes.

Stream	Brook charr	Observed	Mean length(cm)	Brown trout	Observed	Mean length(cm)
Kallån	12	7	13,4	6	1	12,9
Halvförensbäcken	28	3	11,8	0	0	
Långsmaltjärns tillopp	4	1	19,0	0	0	
Hemsjöbäcken	4	2	11,5	0	0	
Uddersjölidbäcken	19	6	12,0	0	0	
Maddmyrbäcken	25	3	10,9	0	0	
Kroktjärnsbäcken	25	5	12,0	0	0	
Rödtjärnsbäcken	2	0	12,3	0	0	
Lammtjuvbäcken	160	2	9,3	0	0	
Lövlidbäcken	37	1	13,9	0	0	
Skavarsbäcken	27	0	12,9	0	0	
Billabäcken	25	0	12,8	17	0	8,8
Järbäcken	24	2	14,1	48	5	14,0
Nipbäcken (east)	25	0	11,3	0	0	
Nipbäcken (west)	44	3	11,2	0	0	
Malmtjärnsbäcken	7	3	10,1	4	0	17,3
Sjunkmyrbäcken	6	2	13,1	0	0	
Rössjöbäcken	1	0	5,0	51	4	10,1

Obstacles

The inventory showed that brook charr had passed slopes as steep as 22% (25m long). Charr had also ascended a 1,3m vertical fall and complex falls up to 1,15m high. Measures made in ArcGIS showed that sections with gradients up to 24% (21m long) and 31% (16m long) had been ascended (Table 5).

Obstacles identified as barriers to further invasion were found in five streams (table 4). The barriers in three of the streams were subsurface stream flow through bolder areas that were from 3,5 to more than 100m long. A 65m long flat rock with a gradient of 22,6% stopped the invasion in Billabäcken. Uddersjölidbäcken was jammed with a four-meter long plug of debris and sediment. As can be seen in figure 2, the invasion rate in streams with obstacles that were identified as barriers to further invasion was significantly lower than in the streams without barriers (Mann-Whitney U test, p= 0,013).

Table 4. Definition of the absolute barriers to further invasion.

Stream	Barrier	Length (m)	Height (m)
Billabäcken	Flat rock	65	15
Långsmaltjärns tillopp	Boulder area with subsurface stream-flow	>100	
Kroktjärnsbäcken	Boulder area with subsurface stream-flow	70	
Maddmyrbäcken	Boulder area with subsurface stream-flow	3,5	0,85
Uddersjölidbäcken	Plug of debris/sediment	4,0	

Based on the inventory of the streams they were divided into three categories (table 5):

1. Streams without absolute barrier to further invasion (n=11).
2. Streams with absolute barrier to further invasion (n=5).
3. Streams in which brook charr has invaded the whole stream (n=2).

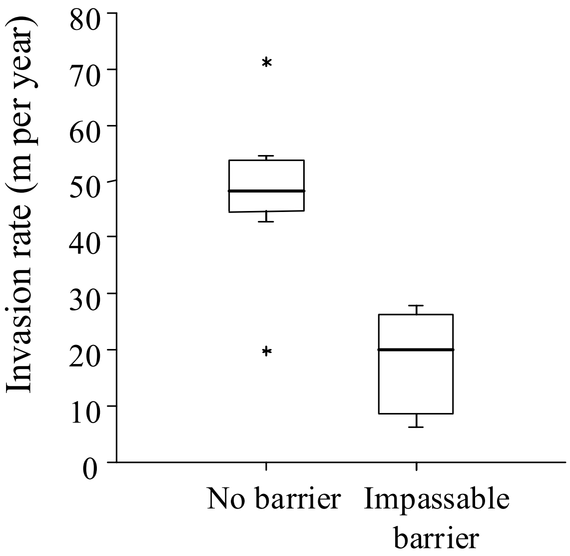

Figure 2 Box-plot of invasion rate (m/year) in the streams with (n=5, mean: 17,76, Std: 9,98) and without (n=8, mean: 47,98, Std: 14,31) absolute barrier to further invasion. (Mann-Whitney U test, p= 0,013).

Invasion rate

Three of the streams without absolute barrier were excluded from the invasion rate analyses. A broken culvert stops the invasion in Sjunkmyrbäcken. In Rössjöbäcken only one brook charr was caught. The upstream invasion in Lövlidbäcken was preceded by a downstream directed invasion from the place of stocking (>5km) to Lövlidbäcken which makes the stream difficult to compare with the others.

The variation in invasion rate between the eight remaining streams without absolute barriers was tested using step-wise multiple linear regression analysis. The variation was best explained by the mean annual discharge (fig. 3) at the site of introduction (T=4,00, p=0,01) and the gradient (fig. 4) of the invaded distance (T=3,07, p=0,028). These factors accounted for 83,1% (T=12,283, p=0,012) of the variation found. The steepest ascended reach, the mean annual discharge in the position of the last caught charr and the number of stockings did not have any significant effect on the invasion rate and were excluded from the analysis. No significant effect of the place of stocking (stream or a lake) or presence of trout in the stream on the invasion rate was found using t-tests.

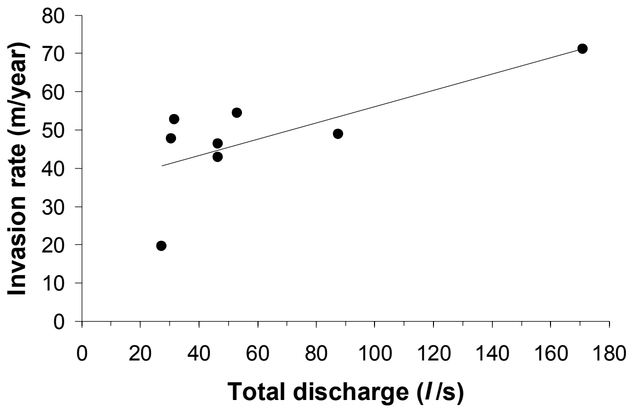

Figure 3. Plot of how invasion rate (m/y) is affected by the total discharge (*l*/s) in the streams without barrier to invasion. p=0,01.

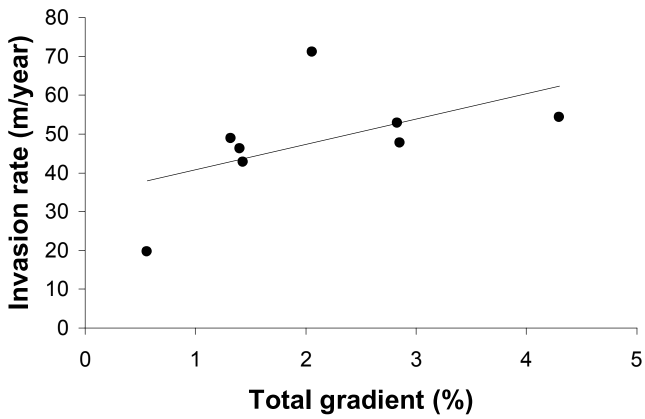

Figure 4. The correlation between total stream gradient and invasion rate in streams with no absolute barrier in front. p=0,028.

Table 5. Stream data. Drainage area, mean annual discharge and stream order at the position of the last caught brook charr. The steepest slope ascended by charr, measured in ArcGIS.

Stream	Absolute barrier to invasion	Drainage area (km^2)	Mean annual discharge (l/s)	Stream-order	Invaded distance (m)	Invasion (m/year)	Gradient (%) invaded distance (GIS)	Gradient (%) steepest ascended slope (GIS)
Lammtjuvbäcken	No	0,68	7,5	1	2796	52,8	2,8	8
Nipbäcken (east)	No	0,47	5,2	1	2311	42,8	1,4	17
Nipbäcken (west)	No	0,56	6,1	1	2499	46,3	1,4	4
Malmtjärnsbäcken	No	0,60	6,6	1	1064	19,7	0,6	2
Järbäcken	No	2,70	29,7	2	3571	48,9	1,3	4
Skavarsbäcken	No	0,87	9,6	2	2882	54,4	4,3	14
Lövlidbäcken	No	1,02	11,3	1	8035	151,6	0,3	31
Sjunkmyrbäcken	No	1,05	11,5	1	2498	48,0	1,4	12
Rössjöbäcken	No	3,30	36,3	2	7900	151,9	1,8	7
Halvförensbäcken	No	0,61	6,8	1	1861	47,7	2,9	4
Kallån	No	2,31	25,4	1	3205	71,2	2,1	24
Långsmaltjärns tillopp	Yes	0,49	5,4	1	1093	26,1	0,8	2
Kroktjärnsbäcken	Yes	1,47	16,2	2	700	13,0	1,4	3
Maddmyrbäcken	Yes	0,23	2,5	1	2022	26,3	1,6	12
Uddersjölidbäcken	Yes	1,06	11,7	2	655	8,5	2,6	5
Billabäcken	Yes	1,43	15,7	2	253	6,2	2,0	9
Hemsjöbäcken	End of stream	0,30	3,3	1	965	16,6	5,4	11
Rödtjärnsbäcken	End of stream	0,34	3,7	1	353	4,6	1,4	7

Discussion

The average upstream invasion rate in the studied streams without obvious obstacles is 48 m/year (Std: 14,3). Adams et al. (2002) investigated brook charr invasion in streams over a 25-year period. In streams without absolute barriers in front, introduced charr had dispersed with an average rate of 39 m/year. In a study by Strange and Habera (1998), introduced rainbow trout (*Oncorhynchus mykiss*) dispersed at a rate of 13-29 m/year. The low invasion rates found in this study and reported in the litterateur indicates that the rate of invasion mainly is an effect of density dependent competition. As the competition gradually increases in the front, brook charr are forced to find new habitats at a rate corresponding to about 48m per year. The invasion probably occurs in pulses rather than as a steady process (Adams et al. 2002). Even though brook charr is known to make long exploratory movements (Gowan and Fausch 1996; Adams et al. 2000, 2001) these may not result in spawning in a new location and are probably of minor importance for the invasion process (Adams et al 2000).

The number of stockings did not affect the invasion rate, although repeated stockings should increase the probability of establishment (Moyle P. B. and Light T. 1996) and thereby invasion rate. If the first stocking is successful and generates a population, then the following stockings might be of minor importance. It may take three or four generations after stocking before a strong population is established and they start to spread. If one generation is approximately five years, the lag-phase would be 15-20 years. Including such a lag phase on the data found here, the average invasion rate increase to 68-80 m/year instead of 48 m/year.

As predicted, the invasion rate increased significantly with mean annual discharge. This may come as no surprise since living space and habitat complexity increases as stream size increase (Rahel and Hubert 1991). Also, larger streams are more likely to have deep pools that provide refuges during periods of thermal stress, low water flows in summer (Matthews et al. 1994) or freeze up during winter (Cunjak 1996). Nevertheless, it was surprising to see the extremely small sizes of the streams that brook charr had invaded in the present study. Ten of the streams in this study had brook charr where the mean annual discharge was less than 10*l*/s. In one case, charr were found in a stream with as low discharge as 2,5*l*/s. This is a lot lower than the smallest streams, containing brook charr, found in the literature; 12*l*/s (Adams et al 2000) and 14*l*/s (Fausch 1989). Rahel and Nibbelink (1999) found that streams containing native brook charr but lacking introduced brown trout tended to be small (<4m wetted width). Small stream sizes may favor a species such as brook charr (Rich et al. 2003), which matures at a small body size and can reproduce in shallow systems with limited spawning habitat (Rachel and Nibbelink 1999). The ability of brook charr to disperse in very small systems can potentially lead to big invasion problems. For example in the stream *Hemsjöbäcken* (3,30*l*/s) brook charr were found all the way up to the source mire (*sphagnum* wetland). About 200 meters across the mire, a stream runs down the other side of the hill into a different drainage area. As brook charr are able to move through mires, (~180m in *Malmtjärnsbäcken*) when water flow is high, they will most likely (if they have not already) spread to the other drainage area. Thus, populations that are thought to be isolated by watersheds may be able to invade new areas via bifurcations, given the right conditions and enough time.

Opposite to my prediction, the invasion rate increased significantly with increasing stream gradient. Most studies agree that the density of charr decline with increasing channel slope (Chrisholm and Hubert 1986; Fausch 1989) and the distribution of steep channel slopes along a stream probably influence brook charr invasion rate by limiting reproductive success or recruitment (Dunham et al. 2003). As no densities were estimated in this study, it is impossible to say whether or not the densities decreased, even if that was the impression. Nevertheless, this study shows that the invasion rate actually increases with the total stream gradient (0,56-4,30%). What makes this increase is hard to tell. Markusson et al. (1997) found that only brook charr, among a number of Swedish fish species (e.g. brown trout and grayling), got more common with increasing stream gradients up over 7% (measured over 1 km). Since steep streams have less suitable habitats for charr than low gradient streams (Bozek and Hubert 1992; Larscheid and Hubert 1992), charr might be forced to pass the steep areas faster. This would explain the higher invasion rate in steeper streams. Gradual stream segments, with good spawning conditions, are often interspersed among the steep reaches and these may facilitate invasions by serving as productive “stepping stones” if colonized by brook charr dispersing upstream through the steeper reaches (Moore et al. 1985; Adams et al. 2000). The highest total gradient was measured in Hemsjöbäcken (5,39%), where the whole stream has been invaded. Gradient of long stream segments from the map gives an indication of a stream’s profile and might be effective for prediction of presence, absence or densities of certain species (Markusson et al. 1997) but it can hardly be used to predict presence or absence of brook charr.

Brook charr were able to disperse through one 21m long slope with a gradient of 24% and one 16m long slope with a gradient of 31%. These are very steep segments with higher ascended gradients than been found in the literature (Fausch 1989; Adams et al. 2000; Rich and McMahon 2003). Vertical waterfalls as high as 1,3m and complex falls up to 1,15m were ascended. Since I never came across a fall higher than 1,3m, no conclusion of the height limit for a barrier can be done.

Five streams had obstacles identified as absolute barriers for further invasion. The brook charr invasion in these streams were significantly slower than in streams without barriers. Three of the streams are blocked for upstream dispersal by subsurface stream-flow through boulder areas (table 4). Thompson and Rahel (1998) found that brook charr (8-22 cm) could move through a 67cm deep and 50cm high rock filled gabion (wire cage). They argue that this was because the barrier did not accumulate enough fine sediments to prevent brook charr from exploiting interstitial spaces. The boulder areas found to be absolute barriers here were a lot larger (3,5 to at least 100m long) and have had plenty of time to accumulate sediment and debris. Shorter passages, smaller than 2m, on the other hand did not seem to be a problem. A broken culvert prevents invasion in *Sjunkmyrbäcken*, but this barrier is probably not an absolute barrier as charr will be able to move upstream if the culvert is repaired. The stream *Uddersjölidbäcken* is jammed with a four-meter long plug of sediment and debris. The very low invasion rate (8,5 m/year) indicates that this has been an obstacle for a long time. The charr in *Billabäcken* are stopped by a 65m long flat rock, slide section with a mean gradient of 22,6%. The last fish was caught beneath a 1,15m high complex fall, which might be the actual barrier but never the less; the slide section just upstream is impossible to ascend. Interesting to note is that none of these five streams had brown trout upstream of the barriers.

It is difficult to define a certain slope gradient as an obvious barrier, if not extremely steep. If a steep section is a barrier or not depends on how waterfalls and other obstacles are distributed in the slope. It may be so if the whole section is a flat rock with no resting-places or if the stream just percolates through boulders and debris. However, if fragmented in stair steps (like a fish ladder) even very steep slopes might be possible to ascend. For example, a fish ladder was built in a flat rock in the stream *Kallån.* This stretch has a gradient of 23% and was probably an absolute barrier, just like the flat rock in *Billabäcken*, before stair steps were made.

Small, steep headwater streams may serve as refuges for native salmonid populations when confronted with introduced species (Fausch 1989; Larscheid and Hubert 1992; Adams 2000), but no such areas with native brown trout were found in this study. The upper part of Kallån was until recently a refuge for trout. The population has been protected against charr invasion by a 1,3m high vertical fall located in a steep stream segment with a gradient of 22%. When the stretch above the waterfall was electro-fished in September 1995 it was stated that no brook charr had ascended the obstacle (Spens *in prep*). This study, however, shows that charr have managed to ascend the fall and now have access to the rest of the stream.

The presence of brown trout in the stream did not significantly affect the invasion rate of brook charr. Moyle and Light (1996) suggests that exotic species are likely to successfully invade a stream or lake if the abiotic factors are appropriate, regardless of other competing species. It has been speculated that cold water temperature and small stream size may favor brook charr over brown trout as they mature at a small body size and thereby can reproduce in shallow systems with limited spawning habitat (Rachel and Nibbelink 1999). Rachel and Nibbelink (1999) found that sites lacking brown trout but containing brook charr tended to be small (<4 m wetted width) and relatively cold streams. Bozek and Hubert (1992) developed an abiotic model that was able to predict the presence of char with 87% probability and absence of trout with 94%. The model classified brook charr as a high elevation, low-gradient, narrow-stream species and brown trout as a low-elevation, low-gradient and wide-stream species. But it is important to stress that these examples are from an area where the brown trout is the non-native and brook charr is the native species. Since brown trout are believed to be better swimmers than brook charr (Peake et al. 1997), they should not have any problems with reaching the upper parts of the systems. It seems possible that the charr, in some cases, have found an empty niche in the upper parts of these small streams and that is why no trout refuges were found.

In two of the streams that were excluded from the statistical analyses, Rössjö- and Lövlidbäcken, the invasion rate was much faster than in the others. Rössjöbäcken, where only one charr was caught, was invaded at a speed of 152 m/year. Since Rössjöbäcken was the largest stream in the study (239*l*/s) this only confirms the conclusion that invasion benefits from high discharge. One can only speculate why just one charr (5cm long) was caught. It seams unlikely that such a small fish would move that long from the rest of the population. But there were two large beaver ponds just downstream that were difficult to fish properly with our equipment. Since Brook charr can exhibit high abundance in beaver ponds (Hilderbrand 1998) it is possible that there were more charr there. Lövlidbäcken has been invaded at a speed of 152 m/year. But the first five-kilometers from the place of stocking were invaded in a downstream direction and only three-kilometers in an upstream direction. It is easier for fish to colonize downstream reaches, rather than to disperse upstream against the flow and potential barriers such as steep cascades and waterfalls (Dunham et al. 2003). This can explain the fast invasion in Lövlidbäcken.

Unfortunately, only eight of the eighteen studied streams could be used in the invasion rate analysis. Since these eight streams had rather similar invasion rates, more replicates would be needed to get statistic significance from factors such as presence of trout or the highest downstream obstacle. It would be interesting to see how fast the invasion rate is in larger streams such as the excluded Rössjöbäcken or larger. It would also be valuable to study streams in which the first introduction is more recent than in the streams in this study. To electro-fish the streams without barrier in a few years to see how the invasion front has moved would also be highly interesting.

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